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Shifting environmental predictors of phenotypes under climate change: a case study of growth in high latitude seabirds

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Climate change is altering species' traits across the globe. To predict future trait changes and understand the consequences of those changes, we need to know the environmental drivers of phenotypic change. In the present study, we use multi-decadal long datasets to determine periods of within-year environmental variation that predict growth of three seabird species. We evaluate whether these periods changed over time and use them to predict future growth under climate change. We find that predictions of trait change could be improved by considering that 1) the timing of environmental factors used to predict traits (predictive-environmental features) can change over time, and 2) the type of predictive-environmental features can change over time. We find evidence of changes in the timing of environmental predictors in all populations studied and evidence for a change in the type of predictor in the studied Arctic murre population. Environmental models of growth predict that warming conditions will decrease growth rates and bird body sizes in two species (black-legged kittiwake *Rissa tridactyla* and glaucous-winged gull *Larus Larus glaucescens*), but not the third (thick-billed murre *Uria lomvia*). Consequently, climate change is likely to decrease fledging rates in the gulls and kittiwakes. Further, we find that sea ice-cover historically predicted murre chick growth well, but no longer does – instead air temperature is now a better predictor of murre growth. Our study highlights a need to investigate whether environmental determinants of trait variation commonly shift in a changing climate and whether such changes have implications for adaptation to novel environments.

Keywords: climate change, development, early-life, growth, sea ice-cover, temperature

Introduction

The relationship between an organism's phenotype and its environment is fundamental to ecology and evolutionary biology (West-Eberhard 2003, Sultan 2015), as

the expression of a particular phenotype in response to environmental conditions (plasticity) can shape both the fitness of an organism and the demography and evolution of a population (Ghalambor et al. 2007, Vedder et al. 2013, Snell-Rood et al. 2018, Rescan et al. 2020). Yet, we are far from accurately predicting phenotypic changes in response to climate change for many species and traits. In particular, it will be important to try to predict impacts on early-life phenotypes because early-life is often a strong selective period, during which many organisms integrate environmental information into a canalized adult phenotype (Williams 1957, Hamilton 1966, English et al. 2016). Therefore, measuring the relationship between early-life phenotypes and environmental conditions is essential in determining the role of the environment in shaping the diversity of phenotypes in a population. Furthermore, environmental change is likely to produce novel environments that may alter patterns of selection experienced during early life and result in reduced recruitment.

In the event of novel environmental conditions in the future we need to know if we can predict organisms' responses to environmental change, and whether the responses will be adaptive (English et al. 2016, Snell-Rood et al. 2018, Bonamour et al. 2019, Simmonds et al. 2019). The population responses to new environments will likely be caused by a complex mix of micro-evolution and phenotypic plasticity. Understanding the associations between environment and early-life growth phenotypes is an important first-step in identifying potential sources of selection or cues for plasticity (Ghalambor et al. 2007, Sultan 2015). After identifying new predictors of traits in longitudinal studies, researchers can evaluate hypotheses related to how these predictors might drive phenotypic change.

The effects of the environment on the developing phenotype can be complex and may include direct effects and indirect effects acting via interactions with other individuals such as parents (Noble et al. 2018, Sauve et al. 2021). Moreover, environmental effects may operate at particular stages, characterized by specific time windows (Kruuk et al. 2015, van de Pol et al. 2016, de Zwaan et al. 2020). The availability of multi-decadal datasets and the development of sliding window statistical approaches are timely assets to identify critical time windows during which particular environmental effects occur (Simmonds et al. 2019).

High latitude populations are ideal study systems in this regard because they are experiencing rapidly warming temperatures that could impact growth directly through overheating, and indirectly through ecosystem changes (Hatch 2013, Gaston and Elliott 2014, Piatt et al. 2020, Choy et al. 2021). Here we investigate the relationship between early-life environmental conditions and growth, a trait frequently associated with immediate and future survival, in three high latitude seabirds. We had four objectives: 1) identify time windows and environmental variables (e.g. air temperature, sea ice-cover) within the breeding season that predict offspring growth, 2) determine if these environmental variables change across years, 3) determine whether the timing of these predictive windows change across years and 4) use this knowledge to make predictions about offspring growth under future climate change. Because environmental conditions are changing quickly in high latitude areas (Moon et al. 2021), we expected that the timing of environmental growth predictors or the predictors themselves might differ between historical and contemporary periods.

Methods

Species, study sites and available data

We used growth data from long-term studies of thick-billed murres *Uria lomvia* (hereafter 'murres') on Coats Island, Nunavut, Canada, and glaucous-winged gulls *Larus glaucescens* and black-legged kittiwakes *Rissa tridactyla* (hereafter, 'gulls' and 'kittiwakes') on Middleton Island, Alaska (Table 1).

Murres

Each year of study on Coats Island (1986–2010; 2017–2018), chicks from ~60 parental pairs were monitored in the colony of ~15 000 pairs (Table 1; Hipfner and Gaston 1999, Gaston et al. 2003, 2005, Gaston and Elliott 2014). One hundred murre eggs were marked during incubation and visited every two days to determine hatching date. If a chick was found wet, it was recorded as hatching on the date of the check and if a chick was pipping it was recorded as hatched the following date. If no information was available a chick was aged using wing length measurements such that the hatch date was recorded as the date of discovery, the previous date and two days prior if the wing length was less than or equal

Table 1. Details of the seabird datasets. Thick-billed murres lay single egg clutches, and we are unable to reliably disentangle the first, second and third egg laid in glaucous-winged gull clutches.

Species	Colony location	n years/chicks	Average number of mass measurements per chick	Study years with chick growth data
Thick-billed murre	Coats Island (Northern Hudson Bay; 62°56′N, 82°0′W)	27/1528	6.08	1986–2010; 2017–2018
Black-legged kittiwake	Middleton Island (Gulf of Alaska; 59°26′N, 146°20′W)	21/1980	First-hatched: 6.88 Second-hatched: 4.5	1998–2018
Glaucous-winged gull	Middleton Island (Gulf of Alaska)	13/1558	2.2	2002–2010; 2012; 2016–2018

to 25, 26–27 and 28–29 mm, respectively. Individuals were banded upon hatching or toe-clipped (if too small to band) and subsequently banded. Chicks were weighed every two to four days. Only mass up to 14 days of age was analyzed because chicks begin to depart from the colony at 15 days, so masses before 15 days of age are unbiased by departure age.

Gulls

Two gull plots (each ~1000 m^2, and encompassing 50–100 nests) were monitored each year of study (2002–2010; 2012; 2016–2018; total population on Middleton ~10 000 birds, Denlinger 2006). Gull nests were marked and checked every four days to determine approximate laying and hatching dates. If a chick was found wet it was recorded as hatching on the date of the check, but if a chick was dry the hatch date was recorded as the mid-point date between check dates. Finally, if a chick was pipping the hatch date was recorded as date after the check. Chicks were banded with a temporary plastic band with a short letter and number sequence to identify individuals. Attempts were made to capture chicks every four days after first discovery, but because chicks can wander from the nest soon after hatching and some chicks avoid capture, the majority of chicks were not weighed at each four-day interval (~2.2 measurements taken per chick; Table 1).

Kittiwakes

On Middleton Island, ~60–400 breeding pairs of kittiwakes that were part of a larger colony of ~15 000 birds were monitored annually in an abandoned radar tower (Gill and Hatch 2002). Birds at the radar tower construct their nests on wooden shelves that have been built in parallel rows on the exterior of the tower. One-way glass panel windows are set in the interior of the tower and can be used to observe each nest from within the tower, and can be removed to handle nestlings. Nests were checked twice daily (9:00 and 18:00 h) throughout the season to record laying and hatching. Eggs hatch asynchronously within clutches, with an average difference of ~1.6 days between the first and second laid egg (Merkling et al. 2016). In each year of the study, the first-hatched and second-hatched chicks were marked with a nontoxic colour marker to distinguish chick rank, and were banded at five days post-hatch for individual identification. Chicks were weighed every five days from hatching to 40 days (i.e. close to fledging). Mass was weighed to the nearest 0.1 g using an electronic scale. As several experiments have been conducted on the nests in the past (Merkling et al. 2016), we excluded data from any chicks that had been experimentally manipulated.

Environmental variables

We evaluated three environmental variables that potentially influence chick growth for some or all seabird datasets: 1) sea-surface temperature, because it frequently reflects the community composition and abundance of prey species for seabirds (Furness 2016); 2) air temperature, because it could improve or worsen thermal conditions for growing chicks, it is associated with growth in kittiwakes (Sauve et al. 2022), and warm temperatures contribute to egg-losses and adult mortality in murres at Coats Island (Gaston and Elliott 2013); and 3) sea ice-cover (for murres), because it is an indicator of a regime shift in the marine ecosystem near Coats Island and has been associated with timing of laying and chick mass at 14-days of age (Gaston et al. 2003, 2005, Gaston and Elliott 2014). We ran analyses for sea ice-cover, sea-surface temperature and air temperature for murres, but only present results for sea ice-cover and air temperature in the main text because sea ice-cover and sea-surface temperature are closely correlated in the spring before and during ice breakup (Supporting information).

Because we expected that sea-surface temperature and sea ice-cover affect prey availability, we used sea-surface temperature and sea ice-cover variables averaged across an area that approximately reflects the foraging range of each species. For murres all pixels within 60 km of Coats Island were averaged each day for sea ice-cover. For kittiwakes and gulls, all pixels within 100 or 50 km respectively of Middleton Island were averaged each day for sea-surface temperatures (Mallory et al. 2018). We used ver. 2 of the advanced very high-resolution dataset (AVHRR) daily sea-surface temperature or sea-ice concentration data from the National Oceanic and Atmospheric Administration (NOAA) National Climatic Data Center (NCDC; https://iridl.ldeo.columbia.edu/SOURCES/.NOAA/.NCDC/.OISST/.version2/.AVHRR/). Air temperatures for Coats Island were collected from the Coral Harbour weather station (~100 km from the murre growth plots; https://climate.weather.gc.ca). Elliott and Gaston (2015) found that daily maximum and minimum air temperature at Coats Island and Coral Harbour are correlated ($R^2 = 0.6$ for both parameters), suggesting that air temperatures at Coral Harbour may be used as a proxy for conditions at Coats Island. Air temperatures for Middleton Island were collected from an airport weather station situated ~2 km from the kittiwake radar tower and gull plots (www.ncdc.noaa.gov/cdo-web).

Statistical analyses

Models of growth

We modelled all growth patterns using Bayesian mixed models with the R package 'brms', which uses the 'Stan' software (Bürkner 2017, Stan Development Team 2019). In all models, we added chick identity and year as random effects for each growth parameter. For all analyses, our biological traits of interest were the individual deviations from the mean population-level estimates of growth curve parameters (for murres; Intercept and Slope; for kittiwakes and gulls, Asymptote, maximum growth rate and timing of maximum growth rate). Because we only used data from the approximately linear part of the growth curve for murres, we modelled murre growth as a linear function of age, the parameters of interest being the intercept and slope of the regression. We used linear mixed models for murres with age

as a fixed effect predictor. Age in days was population mean centred for murres so that the intercept of the regression is the estimated mean mass of a chick during growth and the slope is the estimated mean daily mass change. Because the data span the entirety or most of the chick growth phase for kittiwakes and gulls, we used non-linear mixed models (the unified Richard's curve) for gulls and kittiwakes. The unified Richard's curve is a reparameterization of the Richard's curve, which is a generalized version of a logistic function providing estimations of the relative maximum growth rate, the age at maximum growth and the asymptote or maximum size reached during growth (Sugden et al. 1981, Tjørve and Tjørve 2017). We choose the Richard's curve because it is flexible and can take the shape of many commonly used models of determinate growth (Tjørve and Tjørve 2017). Details of model priors, the extraction of individual deviations, and an analysis of temporal changes in growth parameters are provided in the Supporting information.

Sliding window analyses

We performed sliding window analyses using the R package 'climwin' (van de Pol et al. 2016). A sliding window analysis identifies a time window for which an environmental variable of interest best explains variation in a measured biological trait. We used relative windows that assume each individual record will be impacted by climate at different times relative to the timing of the biological trait. The sliding window analysis varies the start and duration of windows in increments of days. We used it to compare linear and quadratic relationships between the mean, minimum and maximum values of climate for a given time window and individual estimates of model parameters. We evaluate air temperature, sea ice-cover (murres only) and sea-surface temperature for murres, gulls and kittiwakes in a time-period up to 100, 150 and 120 days before measurement of chicks, when they would be 14, 50 and 40 days old (roughly fledging date), respectively. The length of our time periods were chosen to encompass prelaying, follicle development, incubation and growth (Roudybush et al. 1979, Astheimer and Grau 1990). For our interpretation of windows, we have binned the windows identified by our analysis into these time periods. Our process of selection for climwin models can be found in the Supporting information.

Environmental models of growth

The climatic windows identified by climwin were fitted in a model that estimated the statistical effects of each window on all growth curve parameters. If an identical window was detected for two or more growth parameters, the effect of that window was only evaluated once in the growth models. First, we ran separate models for air temperature, sea-surface temperature (gulls and kittiwakes only) and sea ice-cover (murres only). Finally, we ran a model that retained only fixed effects with credible intervals that did not span zero in sea-surface and air temperature models, and combined them into one model. We used an information criterion (LOOIC) derived from approximate leave-one-out cross-validation using Pareto-smoothed importance sampling to compare and evaluate the predictive performance (PSIS-LOO (Vehtari et al. 2017)). Models with a difference in LOOIC values > 5 were considered improvements in model fit.

Timing changes in determinant windows between historical and contemporary periods

We evaluated whether windows detected by the sliding window analysis changed throughout the study period for each species. To do this, we ran the sliding window described above but ran the analyses on each dataset split into two subsets (Supporting information). For each dataset we call the older subset the 'historical' period and the more recent subset the 'contemporary' period. We split the Coats Island dataset: 1) before and after 1995, corresponding to a marked discontinuity in sea ice and food web characteristics (Gaston and Hipfner 1998, Gaston et al. 2012, Provencher et al. 2012), and 2) before and after 1999 to compare the 1995-split to an analysis of the data subsets with similar sample sizes. We included an equal sample size comparison in addition to a comparsion based on an environmental shift for the murres to be consistent with the protocols for the other two species (below) and to include a comparison where differences in window identification between subsets are less likely to be caused by differences in sample size. The ocean regime near Middleton Island is more cyclical than that at Coats Island (Hatch 2013). Consequently, we only split the kittiwake and gull datasets from Middleton once to retain roughly equal sample sizes in the historic and contemporary periods (Supporting information). If we retained a window in both the historical and recent data subsets, we compared the median start and end of the top 95% models for that variable (sea-surface temperature, air temperature or percentage sea ice-cover). The top 95% of models are those that, when their Akaike weights are summed, encompass 95% of the sum of all Akaike weights for models evaluated in the sliding window analysis (Bailey and van de Pol 2016, van de Pol et al. 2016). If the median start and end dates did not overlap between the two data subsets, we considered this support for a shift in the time period of environmental variation that best predicts chick growth. For all data subsets (historical, contemporary and across the entire dataset) we calculated Bayes R^2 from linear models run in 'brms' with each growth parameter as the response and all windows identified for a specific subset by our sliding window analysis as predictors (Gelman et al. 2018).

Predicting future growth

We used the environmental growth models to make predictions about chick growth in a hypothetical environment altered by climate change. We made predictions based on future scenarios of high and low emission scenarios for 2080 (Intergovernmental Panel on Climate Change 2018). The low emissions future corresponded to a 2.2°C increase in air temperatures, a 0.75°C increase in sea-surface temperatures and a 30% decrease in sea ice-cover. The high emissions future corresponded to an 8.3°C increase in air temperatures,

a 1.25°C increase in sea-surface temperatures and a 70% decrease in sea ice-cover for murres. All air temperature and sea ice-cover predictions are estimates derived from Collins et al. (2014) and correspond to estimates for ~60°N latitudes in the year 2080. Sea-surface temperature predictions are estimates derived from Ruela et al. (2020) and correspond to estimate changes predicted in the Gulf of Alaska. The low emission future corresponds to warming under representative concentration pathway 2.6 (RCP2.6; path required to keep global warming below 2°C), and the high emission future corresponds to warming under representative concentration pathway 8.5 (RCP8.5; unimpeded emissions scenario).

Results

Changes in growth over time

On average murres chicks were larger at the end of the study but did not have a clear change in growth rate over the course of study (Fig. 1a, Supporting information). Gull chicks in the latest years tended to reach the lightest asymptote (Fig. 1b). The timing of maximum growth in gulls was non-linear such that chicks growing in the middle of the study were starting maximum growth at ~18–20 days of age, while chicks at the end and beginning of the study started maximum growth at a ~13–15 days of age (Fig. 1b, Supporting information). On average, both first-hatched and second-hatched kittiwakes grew more slowly, started maximum growth at an older age, and reached a lighter asymptote at the end of the study compared to the beginning (Fig. 1c, d, Supporting information).

Climate and growth

In breeding seasons with a higher maximum sea ice-cover, murre chicks grew more quickly (Fig. 2a, b), and when maximum air temperatures were warmer during the incubation/growth period, murres tended to grow more quickly as well (Fig. 2c, d). Warmer conditions were

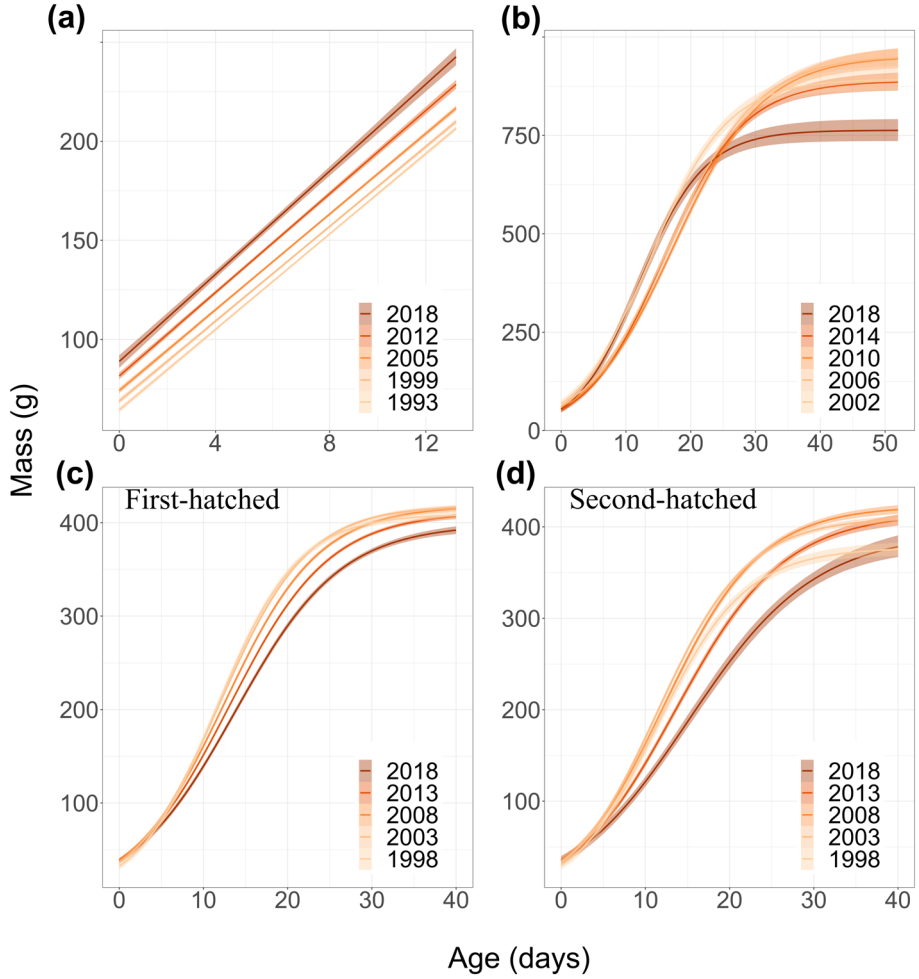

Figure 1. Model predicted changes in growth over time for (a) murres, (b) gulls, (c) first-hatched kittiwakes and (d) second-hatched kittiwakes. For each species predicted growth curves with associated 95% credible intervals (shaded areas) are displayed for the beginning and end year of each study and three evenly spaced sequential years between the start and end of the study. Details of models are presented in the Supporting information.

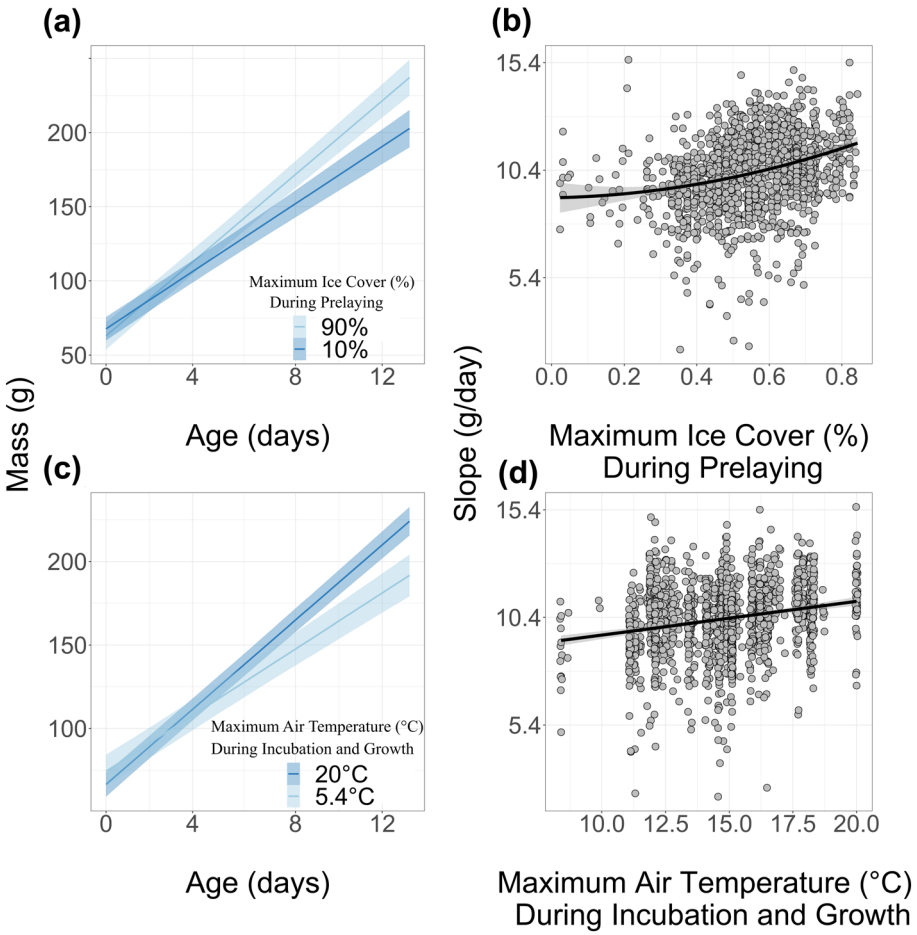

Figure 2. Model predicted effects of (a) maximum sea ice-cover during prelaying and (c) maximum air temperature during incubation and growth, and scatter plots of individual growth slopes (g day^{-1}) across (b) maximum sea ice-cover during prelaying and (d) maximum air temperature during incubation and growth of murre chicks. Individual estimates in graphs on the right (b, d) are the summed annual and individual group effects estimated in our baseline linear mixed effect model and they do not account for estimate error (Hadfield et al. 2010, Houslay and Wilson 2017), therefore the plotted relationships are just for visualization of effects identified in our sliding window analysis. Details of the model are presented in the Supporting information.

associated with slower growing and smaller gull chicks, and second-hatched but not first-hatched kittiwake chicks. Gulls grew more slowly and started maximum growth at an older age when maximum air temperatures during incubation and growth were warmer (Supporting information). None of the environmental models for growth in first-hatched kittiwakes improved model fit compared to the baseline model (Supporting information). Second-hatched kittiwakes grew more slowly, started maximum growth at an older age, and reached a lower asymptote when minimum air temperatures during the breeding season were warmer (Fig. 3a–d).

Changes in windows over time

In all three species, we found evidence of temporal shifts in the timing of predictors identified by our sliding window analysis (Fig. 4, 5 and 6). Variation in murre growth parameters was better explained by environmental windows in contemporary periods, while in gulls and kittiwakes there was heterogeneity across growth traits in variation explained by windows in historic and contemporary periods (Table 2). The periods of sea ice-cover identified by the sliding window analysis of average murre mass tended to be similar before and after 1995, but for growth rate the windows shifted from the prelaying period to encompass follicle development and incubation after 1995 (Fig. 4a). The periods of air temperature identified by the sliding window analysis shifted from the incubation and growth period to the prelaying stage after 1995 (Fig. 4b). In the data subset of murre growth encompassing 1986–1994, only sea ice-cover windows were retained as predictors of chick growth, and only a single air temperature window was retained in the analysis of murre growth after 1994 (Fig. 4a, b).

Sea-surface temperature windows that predicted maximum growth rate and timing of maximum growth rate remained similar before and after 2009 for gulls (Fig. 5a). The sea-surface temperature window that predicted the asymptote of gull mass shifted from prelaying/incubation to

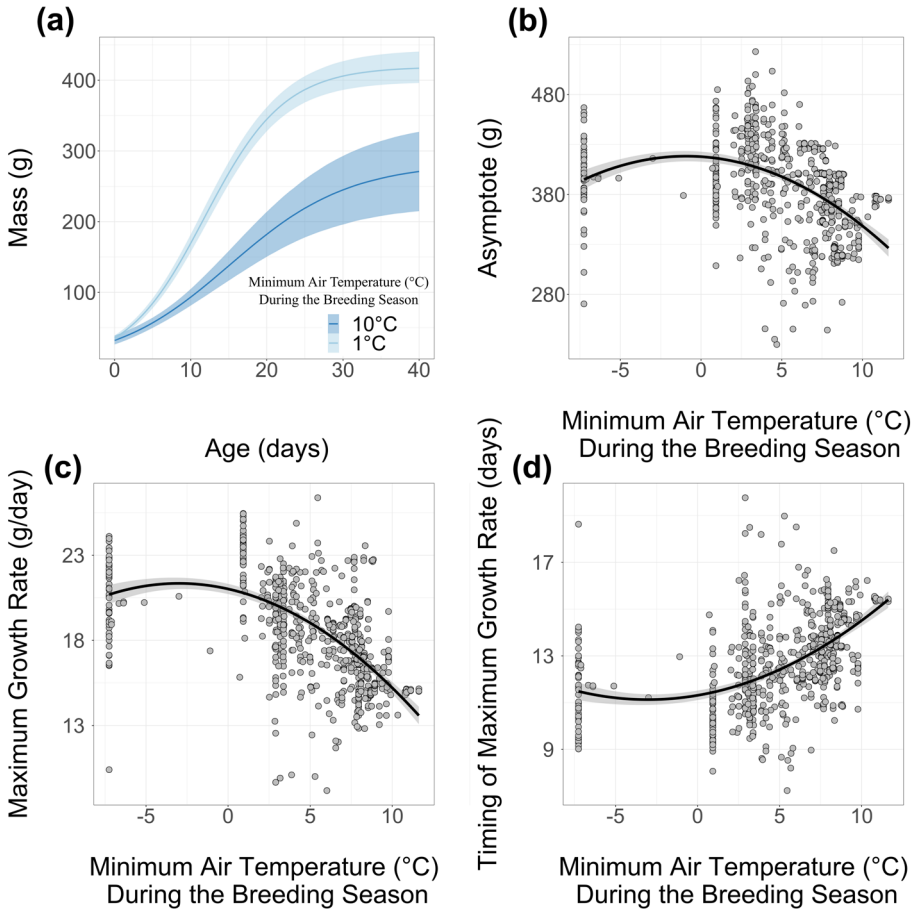

Figure 3. Model predicted effects of (a) maximum air temperature during the breeding season alongside the scatter plots of (b) individual asymptotes (g), (c) maximum growth rate (g day^{-1}) and (d) the timing of maximum growth rate of second-hatched kittiwake chicks, across minimum air temperature during the breeding season. Individual estimates in scatterplots (b–d) are the summed annual and individual group effects estimated in our baseline linear mixed effect model and they do not account for estimate error (Hadfield et al. 2010, Houslay and Wilson 2017), therefore the plotted relationships are just for visualization of effects identified in our sliding window analysis. Details of the model are presented in the Supporting information.

the growth period after 2008. Only the window of sea-surface temperature that predicted the asymptote was retained for the model of gull growth before 2009, while no windows of sea-surface temperature were retained in the model of gull growth after 2009 (Fig. 5). Windows of air temperature that predicted maximum growth encompassed prelaying before and after 2009 but shifted to later in the prelaying period after 2009. The air temperature window that best predicted the timing of maximum growth shifted from the prelaying to growth period (Fig. 5b).

Sea-surface temperature windows that best predicted the timing of maximum growth rate and maximum growth rate of first-hatched kittiwakes shifted from intervals during incubation and growth to a prelaying period after 2007 (Fig. 6a). Air temperature windows that predicted growth parameters of first-hatched kittiwakes remained similar except for windows that predicted the timing of maximum growth, which shifted from a period during growth to a period during prelaying (Fig. 6c). None of the windows identified in the sliding window analysis for any data subset were retained in the model selection for growth of first-hatched kittiwakes (Fig. 6a, c). Almost all sea-surface and air temperature windows that predicted maximum growth or timing of maximum growth in second-hatched chicks tended to overlap or encompass the same growth periods (Fig. 6b, d). However, similarly to first-hatched chicks, the sea-surface temperature windows that best predicted maximum growth and timing of maximum growth shifted to the prelaying period after 2007 in second-hatched kittiwake chicks (Fig. 6b).

Prediction of future growth

Under high emission scenarios large impacts of climate change on growth are predicted for gulls and second-hatched kittiwakes. No environmental windows were retained for models of growth for first-hatched kittiwakes, limiting our ability to make predictions about first-hatched kittiwake chicks in a warming environment (Fig. 6a, c). Under a scenario of high effort to reduce emissions (RCP2.6), the models predicted little impact of warming on chick growth

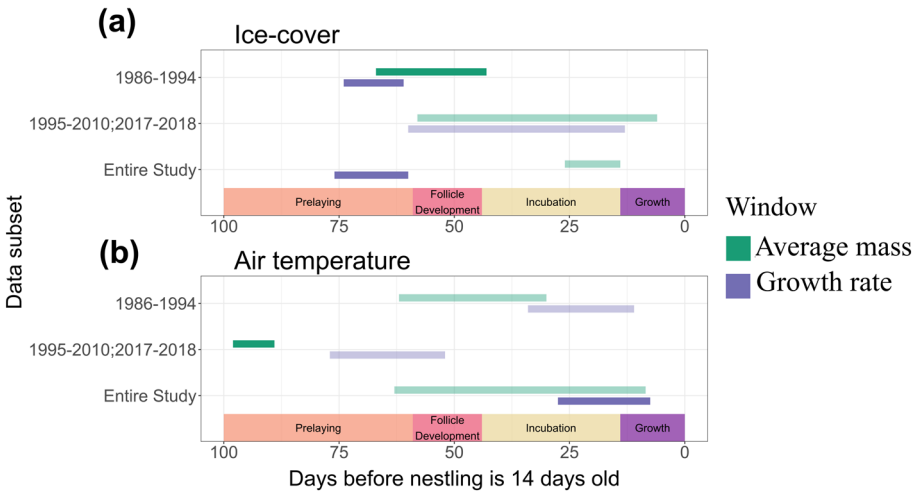

Figure 4. Windows identified in our sliding window analysis as the best predictors of either the intercept (average mass; g) or slope (growth rate; g day^{-1}) of murre growth. Each bar indicates the median start and end of the top 95% models for a given variable (sea-surface temperature, air temperature or percentage sea ice-cover). The top 95% of models are those that when their Akaike weights are summed together encompass 95% of the sum of all Akaike weights for models evaluated in our sliding window analysis (Bailey and Pol 2016, van de Pol et al. 2016). Windows for three data subsets are shown: a historical period (1986–1994, top of y-axis), a contemporary period (1995–2010, 2017–2018; middle of y-axis) and the entire study period (1986–2010, 2017–2018; bottom of y-axis). For each data subset and weather variable the upper teal bar indicates the median start and end of windows that best predict the average mass of murre growth and the purple bar below indicates the start and end of a window that predicts the growth rate of murre growth. Bolded bars were retained in our model selection process and faded bars were not. Details of each model are in the Supporting information. Details of models for murres split before and after 1999 are in the Supporting information.

of murres, gulls or second-hatched kittiwakes (Fig. 7). Under high emissions (RCP8.5), the models predicted limited effects on murres (Fig. 7a) and a greater effect on the growth of gulls and second-hatched kittiwakes (Fig. 7b, c). The models suggest that warming conditions under a high emissions scenario will result on average in slower growing and lighter asymptotic masses for gulls and second-hatched kittiwakes.

Discussion

We applied sliding window analyses combined with long-term growth data to identify specific windows of environmental variation associated with growth of three seabird species. We found 1) windows during the breeding season that predict variation in growth for each species, 2) that the environmental

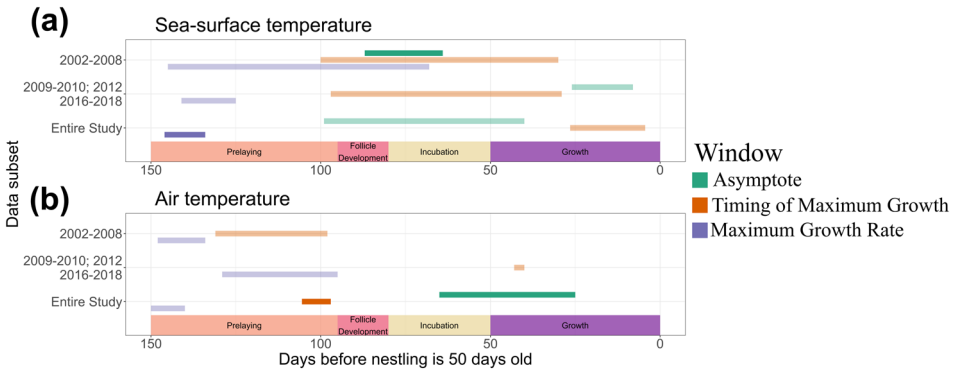

Figure 5. Windows identified in our sliding window analysis as the best predictors of either the asymptote, timing of maximum growth or maximum growth rate of gull growth. Each bar indicates the median start and end of the top 95% models for a given variable (sea-surface temperature or air temperature). The top 95% of models are those that when their Akaike weights are summed together encompass 95% of the sum of all Akaike weights for models evaluated in our sliding window analysis (Bailey and Pol 2016, van de Pol et al. 2016). Windows for three data subsets are shown: a historical period (2002–2008; top of y-axis), a contemporary period (2009–2010, 2012, 2016–2018; middle of y-axis) and the entire study period (2002–2010, 2012, 2016–2018; bottom of y-axis). For each data subset and weather variable the upper teal bar indicates the median start and end of windows that best predict the asymptote of gull growth, the middle yellow bar indicates the median start and end of windows that best predict the timing of maximum growth, and the purple bar below indicates the start and end of a window that predicts the maximum growth rate. Bolded bars were retained in our model selection process and faded bars were not. Details of each model are detailed in the Supporting information.

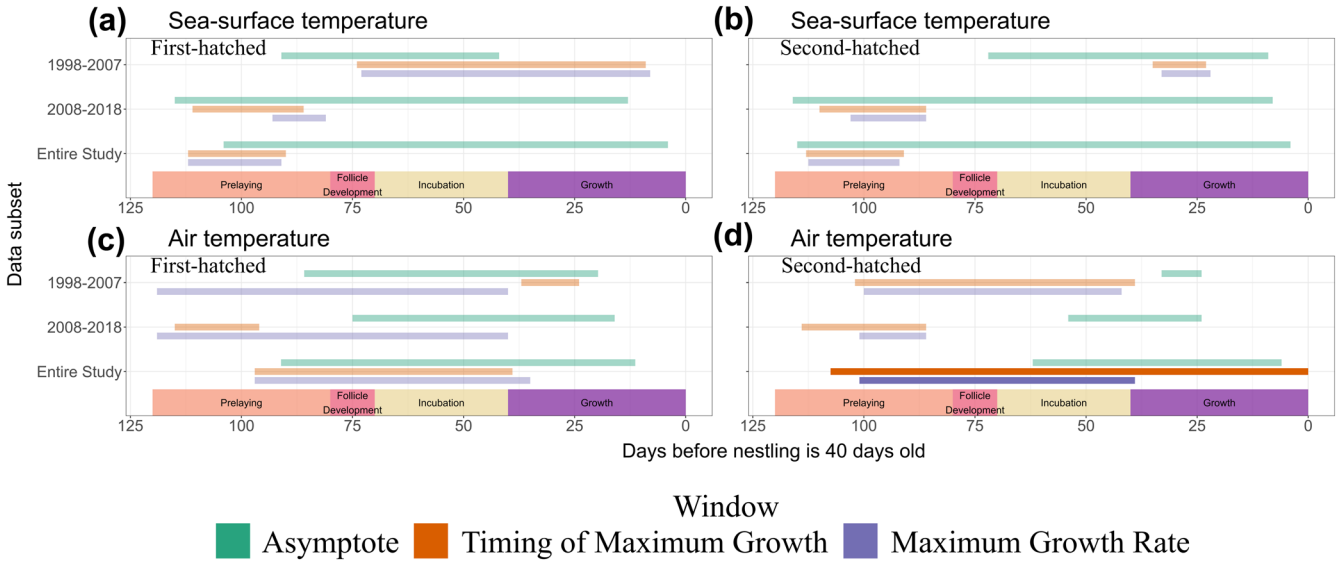

Figure 6. Windows identified in our sliding window analysis as the best predictors of either the asymptote, maximum growth rate or slope of kittiwake growth. Each bar indicates the median start and end of the top 95% models for a given variable (sea-surface temperature or air temperature). The top 95% of models are those that when their Akaike weights are summed together encompass 95% of the sum of all Akaike weights for models evaluated in our sliding window analysis (Bailey and Pol 2016, van de Pol et al. 2016). Windows for three data subsets are shown: a historical period (1998–2007; top of y-axis), a contemporary period (2008–2018; middle of y-axis) and the entire study period (1998–2018; bottom of y-axis). For each data subset and weather variable the upper teal bar indicates the median start and end of windows that best predicts the asymptote of kittiwake growth, the middle yellow bar indicates the median start and end of windows that best predict the timing of maximum growth, and the purple bar below indicates the start and end of a window that predicts the maximum growth rate. Bolded bars were retained in our model selection process and faded bars were not. Details of each model are detailed in the Supporting information.

variable that best predicts growth can change over time, 3) that the period during which an environmental variable is the best predictor of a growth parameter might also change over time and 4) that future warming should result in poorer growth for gulls and kittiwakes, but not murres.

Biological interpretation of associations between environmental windows and growth

More extensive sea ice-cover during the prelaying period and warmer air temperatures during incubation/growth periods were associated with faster growth in murre chicks. These results are similar to what has been identified through previous analyses of the Coats Island dataset on murres. When ice-extent is the lowest in Hudson's bay the chicks tend to grow more slowly, presumably because ice extent is associated with abundance of preferred prey (artic cod *Boreogadus saida*) in the murre diet (Gaston et al. 2005). Warmer air temperatures might improve thermal conditions for growing chicks, as observed in some other high latitude bird species (McKinnon et al. 2012). But, the benefits of warmer air conditions may be transitory, as adult murres are thought to overheat quickly under excessive heat conditions (Choy et al. 2021). Alternatively, the positive relationship between air temperature and murre growth could reflect increased abundance of the subarctic capelin *Mallotus villosus* that are associated with the 'Atlantification' of North Eastern Hudson's Bay (Provencher et al. 2012).

We found a weak quadratic relationship between the growth rate of gulls and sea-surface temperatures during the prelaying period that suggested warm or cold sea-surface temperatures could result in faster growing chicks (Supporting information). We generally assumed warmer sea-surface temperature conditions are associated with poor foraging near Middleton, but gulls have broad diets and might do well foraging in intertidal zones, scavenging and preying on conspecifics when sea-surface temperatures are warm (Hayward et al. 2020). Consistent with that scenario, the sea-surface temperature during the prelaying period was the best predictor of growth rate (Supporting information). Offspring grow more quickly to a smaller size under warm sea-surface temperatures and warmer air temperatures are associated with smaller asymptotes and a later timing of maximum growth in gull chicks suggesting parents might also alter investment (e.g. via hormones or egg size, Groothuis et al. 2005, Hipfner 2012; Supporting information).

Similar to an earlier analysis on Middleton Island kittiwakes, our results suggest that warmer air temperature predicts poorer growth for second-hatched nestlings (Sauve et al. 2021). Because the observed temperatures did not exceed the thermal neutral zone of kittiwake chicks (Bech et al. 1984), we hypothesize that the air temperature during the breeding season predicts or is associated with favourable or unfavourable ecological conditions correlated with temperatures rather than a direct effect of air temperature on nestlings (e.g. colder conditions are associated with an increased capelin; Hatch 2013).

Table 2. Bayes R^2 values with associated 95% credible intervals in brackets for models of each period and species-specific growth parameters (Gelman et al. 2018). Bayes R^2 values are calculated from models predicting a growth parameter and all significant environmental windows from our sliding window analysis of growth parameters.

Time period		R^2 value	
Murres	Growth rate	Average mass	
Historic	0.07 [0.03, 0.11]	0.14 [0.09, 0.20]	
Contemporary	0.17 [0.14, 0.21]	0.32 [0.28, 0.36]	
Entire	0.07 [0.047, 0.094]	0.25 [0.22, 0.28]	
Gulls	Maximum growth rate	Timing of maximum growth rate	Asymptote
Historic	0.18 [0.13, 0.22]	0.25 [0.20, 0.30]	0.07 [0.04, 0.10]
Contemporary	0.07 [0.04, 0.11]	0.07 [0.04, 0.11]	0.05 [0.02, 0.08]
Entire	0.08 [0.06, 0.11]	0.09 [0.06, 0.11]	0.03 [0.02, 0.05]
Alpha kittiwakes			
Historic	0.54 [0.50, 0.58]	0.37 [0.32, 0.42]	0.05 [0.02, 0.09]
Contemporary	0.46 [0.42, 0.50]	0.25 [0.20, 0.30]	0.24 [0.19, 0.29]
Entire	0.43 [0.40, 0.46]	0.28 [0.24, 0.31]	0.13 [0.10, 0.17]
Beta kittiwakes			
Historic	0.57 [0.52, 0.61]	0.51 [0.46, 0.56]	0.16 [0.10, 0.22]
Contemporary	0.34 [0.28, 0.39]	0.21 [0.15, 0.27]	0.49 [0.44, 0.53]
Entire	0.40 [0.35, 0.44]	0.30 [0.25, 0.34]	0.38 [0.34, 0.42]

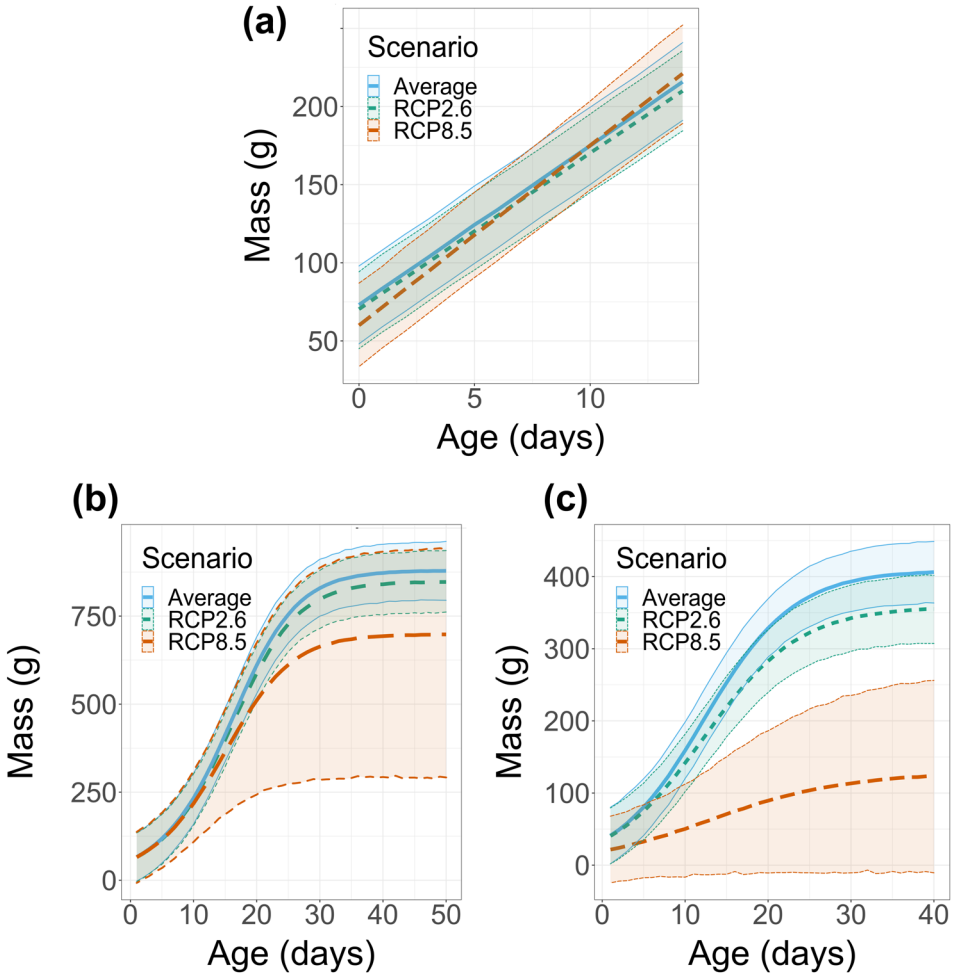

Figure 7. Predicted growth of (a) murres, (b) gulls and (c) second-hatched kittiwakes under average conditions across the study of each species (blue solid line), a low emission climate change scenario (RCP2.6; green short dashed lined), and a high emission climate change scenario (RCP8.5; orange long dashed line). Details of models underlying predictions are in the Supporting information.

Changing predictors of growth across time periods

As global warming induces rapid environmental changes, the environmental predictors of traits can change among years. When testing whether the environmental variables can change over time, we found that sea ice-cover was previously an important predictor of murre growth but may no longer be (Fig. 4; Supporting information). The change in sea ice-cover as the main predictor of growth matches observations that the ecosystem on Coats Island is shifting from an ice-dominated ecosystem to one that is more similar to the Atlantic (Gaston and Hipfner 1998, Gaston et al. 2012, Provencher et al. 2012, Gaston and Elliott 2014).

We did not find evidence for a change in the environmental variables that best predict growth in gulls or kittiwakes (Fig. 5 and 6). The gull and kittiwake data on Middleton Island encompass warm and cool breeding seasons with less of a discontinuous shift in the ecosystem than at Coats Island (Gaston et al. 2012, Hatch 2013). Conditions in the Gulf of Alaska are dominated by the Pacific Decadal Oscillation, which alternates between decades-long phases of cool, wet conditions and warmer, drier conditions (Mantua and Hare 2002). Future studies should try to identify periods of oceanographic and weather conditions that best predict growth across warm years only, to determine when variables are predictors of seabird growth during marine heatwaves.

Temporal changes in the timing of growth predictors

Previous studies have demonstrated that the timing of environmental variables predicting avian phenological events can differ among habitats (Bonamour et al. 2019), but to the best of our knowledge whether the timing of predictors shifts over time has not been evaluated. Shifts of windows may be of concern because they may lead parents to follow unreliable cues and lead to maladaptive timing or offspring number (Temme and Charnov 1987, Visser et al. 2006). In our case study, shifts in growth windows to earlier in the season could indicate offspring reduction is determined early while windows later in the season could indicate abrupt changes occurring later in the breeding season (conditions are more frequently unfavourable late in the season). Abrupt deterioration of breeding season conditions is expected to occur more frequently as late season anomalies and heat-waves are expected to become more common (Piatt et al. 2020).

The timing of the determinants of growth changed over time for all three species studied (Fig. 4, 5 and 6). We did not identify a general pattern in the direction of these shifts within the breeding season. Across all three species we observed environmental windows that moved to earlier periods in the breeding season (e.g. shifted from incubation and growth to prelaying) but also other shifts to later periods (e.g. from prelaying to chick rearing). Growth is a function of parental and chick energy budgets. Predictors identified prenatally could imply indirect parental effects (e.g. egg size, hormones, incubation) while predictors during the postnatal period might suggest impacts of environmental conditions on brooding, foraging rates or the chick thermal environment (Andrew et al. 2017, Andreasson et al. 2018, Sauve et al. 2022), but importantly should be confirmed with experimental approaches (Andrew et al. 2017). Shifts in adult phenology, like the advances observed in the timing of egg laying for Coat's Island murres, also seem likely to play a role in changing predictors of chick growth (Whelan et al. 2022). Determining whether shifts in adult phenology result in shifts in the timing of determinants of chick growth will be an interesting avenue for future research.

Implications of shifting predictors: cues and constraints

Some of the observed associations between climate and chick growth could be the result of growth responses to environmental cues. Adaptive responses to changing environmental conditions are facilitated by temporal autocorrelation. When this autocorrelation is high, conditions in one period can be used to predict conditions in another when natural selection is experienced (Gavrilets and Scheiner 1993, de Jong 1999). To determine if the associations we detected allow adaptive responses we need to know whether they predict future environments (i.e. can the parent environment predict the chick environment or can the chick environment predict the adult environment?). However, we still need to know how changes caused by environmental associations affect survival and reproduction. Empirical work has demonstrated that reproductive hormones and parental care are adjusted to food conditions, number of offspring, partner effort and prolonged prefledging periods (Drent and Daan 1980, Jacobsen et al. 1995, Harding et al. 2009, Whelan et al. 2021).

Our analysis also illustrates some of the difficulties in identifying specific climatic windows. The sliding window analysis detected many windows, but most were not retained in our model selection process, possibly limiting our conclusions on shifts in the timing of environmental predictors. Microclimatic variation or intrinsic factors might better explain some of the variation in growth. Experimental manipulation of chick environments and continued long-term monitoring are needed to determine the importance of specific periods during ontogeny (Andrew et al. 2017, Nord and Giroud 2020, Whelan et al. 2021).

Predicting growth in a warming world

Our growth predictions qualitatively agree with some of the observed changes in murre growth and most of the observed changes in gull and kittiwake growth, suggesting that our identified environmental periods could be driving some of the observed changes in growth across each study period (Fig. 1 and 7). Our climate change predictions for murres suggested limited change in growth, but trends across the study period suggest heavier masses over time in murres. While we discuss some potential causes of the shifting windows above, the shifts highlight an important practical problem to prediction: if predictors continually change, it

becomes more difficult or impossible to make long-term projections. Perhaps a more complex understanding of trait responses to fluctuating conditions is needed. For example, studies attempting to predict microevolutionary change are beginning to model selection on traits as a function of environmental conditions (Chevin et al. 2015, Gamelon et al. 2018, de Villemereuil et al. 2020). But even these models assume the same predictor of selection across years and might, like our window approach suggests, might need continual updates. Further, we could not predict changes in first-hatched kittiwake growth and we hypothesize that this is because parents favour first-hatched nestlings in poor years and, therefore, growth of first-hatched kittiwakes is relatively unperturbed by the range of environmental effects measured in our study. Currently observed environments seem to have a limited impact on first-hatched kittiwakes, but future conditions could nonetheless eventually impact growth of first-hatched kittiwakes. We emphasize this as a key point and limitation for trying to predict kittiwake growth. Finally, it will be important to consider environmental conditions outside the breeding season because migratory conditions might predict unexplained variation or temporal changes in growth (Patterson et al. 2021). While previous investigations have highlighted that changes in phenology and body shape are commonly predicted responses to climate change (Parmesan 2006, Dunn and Møller 2019, Ryding et al. 2021), altered growth patterns and investment in offspring may also be common responses to climate change. Significantly, the slower-growing and smaller chicks predicted for gulls and second-hatched kittiwakes in warm environments portend reduced survival of those chicks, as mass is often a predictor of post-fledging survival (Maness and Anderson 2013). Annual reductions in reproductive effort could have important consequences if later-hatched chicks make up a substantial proportion of the breeding population. For example, of the breeding kittiwakes on Middleton Island approximately 30% are second-hatched chicks. Thus loss of second-hatched kittiwakes could result in a reduced breeding population if they are not replaced by first-hatched kittiwakes.

Conclusions

We found evidence that both the nature and timing of variables correlating with seabird growth can change over time. We identified time periods that predicted poor growth for species with multi-chick broods. We would stress, however, that the stability of environmental predictors over time is unknown, and that instability would compromise our predictive ability and the ability of species to adapt to novel conditions. There remains an important need for research that identifies temporal predictors of phenotypic traits and determines their stability under warming environmental conditions.

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Author contributions

Drew Sauve: Conceptualization (lead); Formal analysis (lead); Funding acquisition (supporting); Methodology (lead); Writing – original draft (lead); Writing – review and editing (equal). **Vicki Friesen**: Conceptualization (supporting); Funding acquisition (equal); Supervision (equal); Writing – review and editing (equal). **Scott Hatch**: Funding acquisition (equal); Project administration (lead); Resources (lead); Writing – review and editing (supporting). **Kyle Elliott**: Conceptualization (supporting); Methodology (supporting); Project administration (equal); Resources (equal); Writing – review and editing (supporting). **A. Charmantier**: Conceptualization (supporting); Funding acquisition (equal); Methodology (supporting); Supervision (equal); Writing – review and editing (equal).

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Data availability statement

Data are available from the Figshare: https://doi.org/10.6084/m9.figshare.19137146 (Sauve et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Andreasson, F., Nord, A. and Nilsson, J.-A. 2018. Experimentally increased nest temperature affects body temperature, growth and apparent survival in blue tit nestlings. – J. Avian Biol. 49: e01620.

Andrew, S. C., Hurley, L. L., Mariette, M. M. and Griffith, S. C. 2017. Higher temperatures during development reduce body size in the zebra finch in the laboratory and in the wild. – J. Evol. Biol. 30: 2156–2164.

Astheimer, L. B. and Grau, C. R. 1990. A comparison of yolk growth rates in seabird eggs. – Ibis 132: 380–394.

Bailey, L. D. and van de Pol, M. 2016. climwin: an R toolbox for climate window analysis. – PLoS One 11: e0167980.

Bech, C., Martini, S., Brent, R. and Rasmussen, J. 1984. Thermoregulation in newly hatched black-legged kittiwakes. – Condor 86: 339–341.

Bonamour, S., Chevin, L.-M., Charmantier, A. and Teplitsky, C. 2019. Phenotypic plasticity in response to climate change: the importance of cue variation. – Phil. Trans. R. Soc. B 374: 20180178.

Bürkner, P.-C. 2017. brms: an R package for Bayesian multilevel models using Stan. – J. Stat. Softw. 80: 1–28.

Chevin, L.-M., Visser, M. E. and Tufto, J. 2015. Estimating the variation, autocorrelation and environmental sensitivity of phenotypic selection. – Evolution 69: 2319–2332.

Choy, E. S., O'Connor, R. S., Gilchrist, H. G., Hargreaves, A. L., Love, O. P., Vézina, F. and Elliott, K. H. 2021. Limited heat tolerance in a cold-adapted seabird: implications of a warming Arctic. – J. Exp. Biol. 224: jeb242168.

Collins, M., Knutti, R., Arblaser, J., Dufresne, J.-L., Fichefet, T., Friedlingstein, P., Gao, X., Gutowski, W., Johns, T., Krinner, G., Shongwe, M., Teballdi, C., Weaver, A. and Wehner, M. 2014. Long-term climate change: projections, commitments and irreversibility. – In: Stocker, T. F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S. K., Boschung, J., Nauels, A., Xia, Y., Bex, V. and Midgley, P. M. (eds), Climate change 2013: they physical science basis contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change. Cambridge Univ. Press, pp. 1029–1136.

de Jong, G. 1999. Unpredictable selection in a structured population leads to local genetic differentiation in evolved reaction norms. – J. Evol. Biol. 12: 839–851.

de Villemereuil, P., Charmantier, A., Arlt, D., Bize, P., Brekke, P., Brouwer, L., Cockburn, A., Côté, S. D., Dobson, F. S., Evans, S. R., Festa-Bianchet, M., Gamelon, M., Hamel, S., Hegelbach, J., Jerstad, K., Kempenaers, B., Kruuk, L. E. B., Kumpula, J., Kvalnes, T., McAdam, A. G., McFarlane, S. E., Morrissey, M. B., Pärt, T., Pemberton, J. M., Qvarnström, A., Røstad, O. W., Schroeder, J., Senar, J. C., Sheldon, B. C., van de Pol, M., Visser, M. E., Wheelwright, N. T., Tufto, J. and Chevin, L.-M. 2020. Fluctuating optimum and temporally variable selection on breeding date in birds and mammals. – Proc. Natl Acad. Sci. USA 117: 31969–31978.

de Zwaan, D. R., Drake, A., Greenwood, J. L. and Martin, K. 2020. Timing and intensity of weather events shape nestling development strategies in three alpine breeding songbirds. – Front. Ecol. Evol. 8: 570034.

Denlinger, L. 2006. Alaska Seabird Information Series (ASIS). – US Fish and Wildlife Service, Migratory Bird Management, Nongame Program.

Drent, R. H. and Daan, S. 1980. The prudent parent: energetic adjustments in avian breeding 1. – Ardea 55: 225–252.

Druckenmiller, M. L., Thoman, M. L. and Moon, T. A. (eds) 2022. Arctic Report Card 2022.

Dunn, P. O. and Møller, A. P. 2019. Effects of climate change on birds. – Oxford Univ. Press.

Elliott, K. H. and Gaston, A. J. 2015. Diel vertical migration of prey and light availability constrain foraging in an Arctic seabird. – Mar. Biol. 162: 1739–1748.

English, S., Fawcett, T. W., Higginson, A. D., Trimmer, P. C. and Uller, T. 2016. Adaptive use of information during growth can explain long-term effects of early life experiences. – Am. Nat. 187: 620–632.

Furness, R. 2016. Impact and effects of ocean warming on seabirds. – In: Laffoley, D. and Baxter, J. M. (eds), Explaining ocean warming. IUCN, pp. 271–288.

Gamelon, M., Tufto, J., Nilsson, A. L. K., Jerstad, K., Røstad, O. W., Stenseth, N. C. and Sæther, B.-E. 2018. Environmental drivers of varying selective optima in a small passerine: a multivariate, multiepisodic approach. – Evolution 72: 2325–2342.

Gaston, A. J. and Elliott, K. H. 2013. Effects of climate-induced changes in parasitism, predation and predator–predator interactions on reproduction and survival of an arctic marine bird. – Arctic 66: 43–51.

Gaston, A. J. and Elliott, K. H. 2014. Seabird diet changes in northern Hudson Bay, 1981–2013, reflect the availability of schooling prey. – Mar. Ecol. Prog. Ser. 513: 211–223.

Gaston, A. J. and Hipfner, M. 1998. The effect of ice conditions in northern Hudson Bay on breeding by thick-billed murres *Uria lomvia*. – Can. J. Zool. 76: 480–492.

Gaston, A. J., Gilchrist, H. G. and Hipfner, J. M. 2005. Climate change, ice conditions and reproduction in an Arctic nesting marine bird: Brunnich's guillemot (*Uria lomvia* L.). – J. Anim. Ecol. 74: 832–841.

Gaston, A. J., Smith, P. A. and Provencher, J. F. 2012. Discontinuous change in ice-cover in Hudson Bay in the 1990s and some consequences for marine birds and their prey. – ICES J. Mar. Sci. 69: 1218–1225.

Gaston, A. J., Woo, K. and Hipfner, J. M. 2003. Trends in forage fish populations in northern Hudson Bay since 1981, as determined from the diet of nestling thick-billed murres *Uria lomvia*. – Arctic 56: 227–233.

Gavrilets, S. and Scheiner, S. M. 1993. The genetics of phenotypic plasticity. V. Evolution of reaction norm shape. – J. Evol. Biol. 6: 31–48.

Gelman, A., Goodrich, B., Gabry, J. and Vehtari, A. 2018. R-squared for Bayesian regression models. – Am. Stat. 73: 307–309.

Ghalambor, C. K., McKay, J. K., Carroll, S. P. and Reznick, D. N. 2007. Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. – Funct. Ecol. 21: 394–407.

Gill, V. A. and Hatch, S. A. 2002. Components of productivity in black-legged kittiwakes *Rissa tridactyla*: response to supplemental feeding. – J. Avian Biol. 33: 113–126.

Groothuis, T. G. G., Müller, W., von Engelhardt, N., Carere, C. and Eising, C. 2005. Maternal hormones as a tool to adjust offspring phenotype in avian species. – Neurosci. Biobehav. Rev. 29: 329–352.

Hadfield, J. D., Wilson, A. J., Garant, D., Sheldon, B. C. and Kruuk, L. E. B. 2010. The misuse of BLUP in ecology and evolution. – Am. Nat. 175: 116–125.

Hamilton, W. D. 1966. The moulding of senescence by natural selection. – J. Theor. Biol. 12: 12–45.

Harding, A. M. A., Kitaysky, A. S., Hall, M. E., Welcker, J., Karnovsky, N. J., Talbot, S. L., Hamer, K. C. and Grémillet, D. 2009. Flexibility in the parental effort of an Arctic-breeding seabird. – Funct. Ecol. 23: 348–358.
Hatch, S. A. 2013. Kittiwake diets and chick production signal a 2008 regime shift in the northeast Pacific. – Mar. Ecol. Prog. Ser. 477: 271–284.
Hayward, J. L. and Verbeek, N. A. 2020. Glaucous-winged gull *Larus glaucescens*, ver. 1.0. – In: Billerman, S. M. (ed.), Birds of the world. Cornell Lab of Ornithology. It is accessed from the online encyclopedia here: https://doi.org/10.2173/bow.glwgul.01
Hipfner, J. M. 2012. Effects of sea-surface temperature on egg size and clutch size in the glaucous-winged gull. – Waterbirds 35: 430–436.
Hipfner, J. M. and Gaston, A. J. 1999. The relationship between egg size and posthatching development in the thick-billed murre. – Ecology 80: 1289–1297.
Houslay, T. M. and Wilson, A. J. 2017. Avoiding the misuse of BLUP in behavioural ecology. – Behav. Ecol. 28: 948–952.
Intergovernmental Panel on Climate Change 2018. Global warming of 1.5°C. – Cambridge Univ. Press.
Jacobsen, K.-O., Erikstad, K. E. and Saether, B.-E. 1995. An experimental study of the costs of reproduction in the kittiwake *Rissa tridactyla*. – Ecology 76: 1636–1642.
Kruuk, L. E. B., Osmond, H. L. and Cockburn, A. 2015. Contrasting effects of climate on juvenile body size in a Southern Hemisphere passerine bird. – Global Change Biol. 21: 2929–2941.
Mallory, M. L., Gaston, A. J., Provencher, J. F., Wong, S. N. P., Anderson, C., Elliott, K. H., Gilchrist, G., Janssen, M., Lazarus, T., Patterson, A., Pirie-Dominix, L. and Spencer, N. C. 2018. Identifying key marine habitat sites for seabirds and sea ducks in the Canadian Arctic. – Environ. Rev. 27: 215–240.
Maness, T. J. and Anderson, D. J. 2013. Predictors of juvenile survival in birds. – Ornithol. Monogr. 78: 1–55.
Mantua, N. J. and Hare, S. R. 2002. The Pacific decadal oscillation. – J. Oceanogr. 58: 35–44.
McKinnon, L., Picotin, M., Bolduc, E., Juillet, C. and Bêty, J. 2012. Timing of breeding, peak food availability and effects of mismatch on chick growth in birds nesting in the High Arctic. – Can. J. Zool. 90: 961–971.
Merkling, T., Perrot, C., Helfenstein, F., Ferdy, J.-B., Gaillard, L., Lefol, E., Voisin, E., Hatch, S. A., Danchin, E. and Blanchard, P. 2016. Maternal effects as drivers of sibling competition in a parent–offspring conflict context? An experimental test. – Ecol. Evol. 6: 3699–3710.
Noble, D. W. A., Stenhouse, V. and Schwanz, L. E. 2018. Developmental temperatures and phenotypic plasticity in reptiles: a systematic review and meta-analysis. – Biol. Rev. 93: 72–97.
Nord, A. and Giroud, S. 2020. Lifelong effects of thermal challenges during development in birds and mammals. – Front. Physiol. 11: 419.
Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. – Annu. Rev. Ecol. Evol. Syst. 37: 637–669.
Patterson, A., Gilchrist, H. G., Gaston, A. and Elliott, K. H. 2021. Northwest range shifts and shorter wintering period of an Arctic seabird in response to four decades of changing ocean climate. – Mar. Ecol. Prog. Ser. 679: 163–179.
Piatt, J. F., Parrish, J. K., Renner, H. M., Schoen, S. K., Jones, T. T., Arimitsu, M. L., Kuletz, K. J., Bodenstein, B., García-Reyes, M., Duerr, R. S., Corcoran, R. M., Kaler, R. S. A., McChesney, G. J., Golightly, R. T., Coletti, H. A., Suryan, R. M., Burgess, H. K., Lindsey, J., Lindquist, K., Warzybok, P. M., Jahncke, J., Roletto, J. and Sydeman, W. J. 2020. Extreme mortality and reproductive failure of common murres resulting from the northeast Pacific marine heatwave of 2014–2016. – PLoS One 15: e0226087.
Provencher, J. F., Gaston, A. J., O'Hara, P. D. and Gilchrist, H. G. 2012. Seabird diet indicates changing Arctic marine communities in eastern Canada. – Mar. Ecol. Prog. Ser. 454: 171–182.
Rescan, M., Grulois, D., Ortega-Aboud, E. and Chevin, L.-M. 2020. Phenotypic memory drives population growth and extinction risk in a noisy environment. – Nat. Ecol. Evol. 4: 193–201.
Roudybush, T. E., Grau, C. R., Petersen, M. R., Ainley, D. G., Hirsch, K. V., Gilman, A. P. and Patten, S. M. 1979. Yolk formation in some charadriiform birds. – Condor 81: 293–298.
Ruela, R., Sousa, M. C., deCastro, M. and Dias, J. M. 2020. Global and regional evolution of sea surface temperature under climate change. – Global Planet. Change 190: 103190.
Ryding, S., Klaassen, M., Tattersall, G. J., Gardner, J. L. and Symonds, M. R. E. 2021. Shape-shifting: changing animal morphologies as a response to climatic warming. – Trends Ecol. Evol. 36: 1036–1048.
Sauve, D., Charmantier, A., Hatch, S. A. and Friesen, V. L. 2022. Environmental conditions variably affect growth across the breeding season in a subarctic seabird. – Oecologia 198: 307–318.
Sauve, D., Friesen, V. L. and Charmantier, A. 2021. The effects of weather on avian growth and implications for adaptation to climate change. – Front. Ecol. Evol. 9: 569741.
Sauve, D., Friesen, V. L., Hatch, S. A., Elliott, K. H. and Charmantier, A. 2023. Data from: Shifting environmental predictors of phenotypes under climate change: a case study of growth in high latitude seabirds. – Figshare, https://doi.org/10.6084/m9.figshare.19137146.
Simmonds, E. G., Cole, E. F. and Sheldon, B. C. 2019. Cue identification in phenology: a case study of the predictive performance of current statistical tools. – J. Anim. Ecol. 88: 1428–1440.
Snell-Rood, E. C., Kobiela, M. E., Sikkink, K. L. and Shephard, A. M. 2018. Mechanisms of plastic rescue in novel environments. – Annu. Rev. Ecol. Evol. Syst. 49: 331–354.
Stan Development Team 2019. Stan modeling language users guide and reference manual, 2.21. – https://mc-stan.org.
Sugden, L. G., Driver, E. A. and Kingsley, M. C. S. 1981. Growth and energy consumption by captive mallards. – Can. J. Zool. 59: 1567–1570.
Sultan, S. E. 2015. Organism and environment. – Oxford Univ. Press.
Temme, D. H. and Charnov, E. L. 1987. Brood size adjustment in birds: economical tracking in a temporally varying environment. – J. Theor. Biol. 126: 137–147.
Tjørve, K. M. C. and Tjørve, E. 2017. Modelling avian growth with the Unified-Richards: as exemplified by wader-chick growth. – J. Avian Biol. 48: 770–784.
van de Pol, M., Bailey, L. D., McLean, N., Rijsdijk, L., Lawson, C. R. and Brouwer, L. 2016. Identifying the best climatic predictors in ecology and evolution. – Methods Ecol. Evol. 7: 1246–1257.
Vedder, O., Bouwhuis, S. and Sheldon, B. C. 2013. Quantitative assessment of the importance of phenotypic plasticity in

adaptation to climate change in wild bird populations. – PLoS Biol. 11: 1–10.
Vehtari, A., Gelman, A. and Gabry, J. 2017. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. – Stat. Comput. 27: 1413–1432.
Visser, M. E., Holleman, L. J. M. and Gienapp, P. 2006. Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. – Oecologia 147: 164–172.
West-Eberhard, M. J. 2003. Developmental plasticity and evolution. – Oxford Univ. Press.
Whelan, S., Hatch, S. A., Benowitz-Fredericks, Z. M., Parenteau, C., Chastel, O. and Elliott, K. H. 2021. The effects of food supply on reproductive hormones and timing of reproduction in an income-breeding seabird. – Horm. Behav. 127: 104874.
Whelan, S., Hatch, S. A., Gaston, A. J., Gilchrist, G. H. and Elliott, K. H. 2022. Opposite, but insufficient, phenological responses to climate in two circumpolar seabirds: relative roles of phenotypic plasticity and selection. – Funct. Ecol. 36: 1782–1795.
Williams, G. C. 1957. Pleiotropy, natural selection and the evolution of senescence. – Evolution 11: 398–411.